PHYSIOLOGY

SUPRASPINAL CONTROL OF SYNAPTIC PROCESSES IN VISCEROMOTOR REFLEXES

P. G. Kostyuk and N. N. Preobrazhenskii

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By means of the intracellular recording of the potentials of the spinal motor neurons during stimulation of the interoceptive afferent pathways [1], it has been shown that the pathways of the visceromotor reflexes possess a highly complex synaptic organization. In the conditions of an intact nervous system a simultaneous activation of intracentral systems of varying degrees of complexity, the character of whose synaptic action on the different types of motor neurons is not identical, evidently takes place. It may be supposed that among these systems there are some which are associated with activation of the supraspinal structures and others which are purely intraspinal and, in turn, possibly under the tonic inhibitory control of the higher centers. Division of the spinal cord in the thoracic portion considerably facilitates the transmission of interoceptive influences to the motor neurons of the intercostal muscles [3,4]; it may therefore be suggested with full justification that division of this type introduces essential changes into the synaptic processes created by interoceptive impulses in the lumbar motor neurons.

This paper describes the changes arising in the synaptic activation of the motor neurons in response to visceromotor influences in spinal animals and compares them with the corresponding changes in animals with the connections between the spinal cord and the brain left intact.

EXPERIMENTAL METHOD

The synaptic processes in the 5th-6th lumbar segments were investigated in spinal and decerebrate cats by intracellular recording of their potentials using the method described previously [1]. The spinal cord was transected at the level of the 2nd cervical segment, after which the animal was maintained on artificial respiration; decerebration was performed at the anterior border of the posterior colliculi. Additional immobilization was obtained by intravenous injection of Listhenon (4-6 mg/kg body weight). The recordings from the motor neurons began not sooner than 1-2 h after transection; in some experiments, strychnine was also injected in a dose of 100 mg/kg and the synaptic processes were investigated in the conditions of a much higher level of reflex excitability.

EXPERIMENTAL RESULTS

Studies were made of the postsynaptic potentials (PSP) of 31 motor neurons of spinal animals and 24 motor neurons of decerebrate animals, arising in response to stimulation of both the ipsilateral and contralateral splanchnic nerve.

Spinal Animals. The PSP of the investigated motor neurons appeared after a much shorter latent period (Fig. 1) than the PSP of the motor neurons of the animals with an intact central nervous system. The mean length of the latent period of the PSP during ipsilateral stimulation was 13.6 ± 0.8 msec, and during contralateral stimulation 14.5 ± 0.7 msec (varying from 8 to 20 msec). The corresponding values for the intact central nervous system were 31 and 25.7 msec [1]. The PSP itself was also shorter in duration, with a mean length of 53.2 ± 3.8 msec for ipsilateral and 51 ± 3.4 msec for contralateral stimulation.

An important distinguishing feature of the PSP in the spinal cats was their uniformity. In both the flexor and the extensor motor neurons, the afferent wave from the splanchnic nerve generated an excitatory PSP (see Fig. 1). Prolonged inhibitory postsynaptic changes, so characteristic of the extensor motor neurons in animals with an intact brain, were absent in this case. Only in two cases of spinal strychninized cats were weak potentials of hyperpolarization type found; however, because of the presence of considerable extracellular fields in the region of the motor nuclei on the arrival of an afferent wave from the splanchnic nerve, they could not be reliably differentiated from the effects of the extracellular electric field. The shape of the PSP of the motor neurons was largely dependent on the

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*Laboratory of General Physiology, A. A. Bogomolets Institute of Physiology, Academy of Sciences of the UkrSSR, Kiev (Presented by Active Member of the Academy of Medical Sciences of the USSR, V. V. Parin). Translated from Byulleten' Éksperimental'noi Biologii i Meditsiny, Vol. 62, No. 8, pp. 3-7, August, 1966. Original article submitted April 23, 1965.

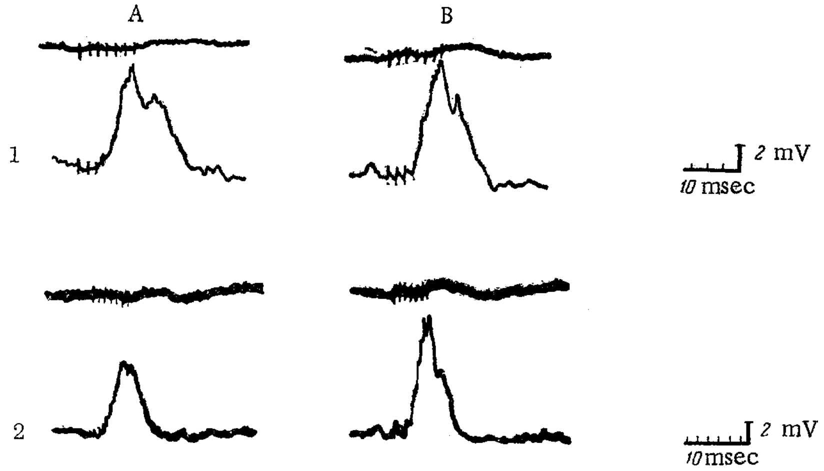

Fig. 1. PSP of flexor (1) and extensor (2) motor neurons during stimulation of the ipsi- (A) and contralateral (B) splanchnic nerves. The top beam in Figs. 1 and 2 is the potential of the dorsal surface of the spinal cord in the investigated segment; the bottom beam is the PSP of the motor neuron. The oscillograms were obtained during a single traverse of the beam.

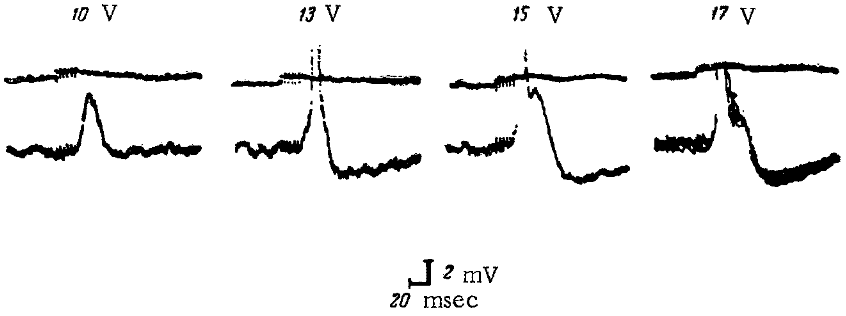

Fig. 2. Relationship between the shape of the PSP of a flexor motor neuron and an increase in the strength of the stimulating current during stimulation of the ipsilateral splanchnic nerve. The first three oscillograms were obtained during a single traverse of the beam, the last by superposing ten traverses of the beam, in step with the stimulation.

strength of stimulation of the splanchnic nerves. Overthreshold stimulation of the central end of the ipsilateral splanchnic nerve caused a simple excitatory PSP in the motor neuron (Fig. 2), which generated a spreading action potential if the amplitude of stimulation was increased. A further increase in the strength of the stimulating current led to the appearance of the second phase of the PSP, which from its time parameters may be regarded as the addition of excitation evoked by group B fibers.

Because of the faster appearance of the excitatory PSP (EPSP) and of their shorter course, the generation of the discharges of the motor neurons took place after a much shorter latent period and with much greater synchronization. In some motor neurons, the generation of the spreading impulse took in response to every afferent wave (if, of course, these waves were not sent too frequently) at a strictly constant moment of time after application of the stimulation (see Fig. 2, the last oscillogram).

Injection of strychnine into the spinal animal led to no significant changes in the PSP created in the lumbar motor neurons by the interoceptive wave. The mean length of the latent period of the PSP in response to stimulation of the ipsilateral splanchnic nerve in this case was 17.5 msec (results of the investigation of seven motor neurons) and, consequently, practically the same as the mean length of this period in the animals not receiving strychnine. Strychninization produced only an increase in the amplitude of the PSP and facilitated the appearance of intensive PSPs or discharges of the motor neurons in response to fewer stimuli.

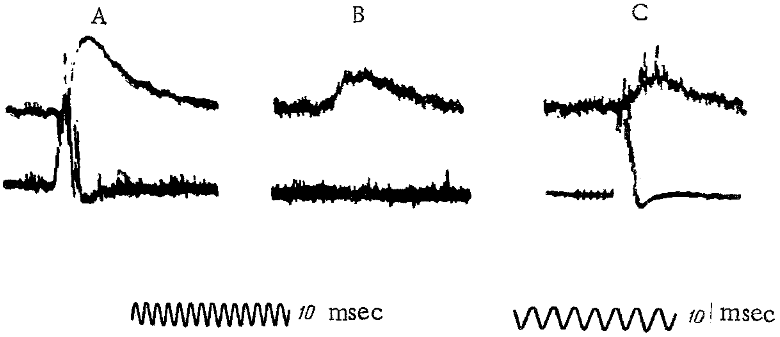

Fig. 3. ETP of a dorsal root (top beam) and reflex discharge of the corresponding ventral root (bottom beam) of the 6th lumber segment of the spinal cord arising in response to stimulation of the ipsilateral splanchnic nerve: A) in an animal with its nervous system intact; B and C) in the same animal after division of the spinal cord in the region of C_2 and after injection of strychnine, respectively.

Division of the spinal cord gave rise not only to the changes in the postsynaptic processes in the motor neurons described above, but also to considerable changes in the course of the prolonged depolarization of the central endings of the afferent fibers produced by the interoceptive wave [2]. The mean length of the latent period of the electrotonic potential (ETP) of the dorsal root, arising in the 6th lumbar segment in response to stimulation of the ipsilateral splanchnic nerve, was shortened in an animal with its nervous system intact from 35.4 to 20.4 msec (Fig. 3B). The ETP of the dorsal root reached a maximum 13.6 sec after its onset, and the time constant of its decline was 53 msec. The depth of depolarization of the afferent endings after division of the spinal cord, with the same strength of stimulation of the nerve, was much less than before division. A considerable increase in the reflex excitability of the spinal cord caused by strychnine did not lead to any significant increase in the strength or duration of this depolarization (Fig. 3C).

Decerebrate Animals. The PSPs appeared in the motor neurons of these animals after a shorter latent period than in the cats with an intact nervous system. The latent period of the PSP in response to stimulation of the ipsilateral splanchnic nerve averaged 16.7 ± 1.7 msec (variation from 13 to 24 msec) and, consequently, it came appreciably closer to that in the motor neurons of the spinal animals.

At the same time, a characteristic feature of these reactions was the well-marked prolonged secondary components (inhibitory PSP — IPSP — in the extensor, EPSP in the flexor motor neurons). The latent periods of these components were indistinguishable from those in animals with an intact nervous system. Depolarization of the central endings of the somatic afferent fibers in response to stimulation of the splanchnic nerve of the decerebrate cats also had time characteristics close to those of the intact animals.

DISCUSSION OF RESULTS

The results described above show that there exists in the spinal cord a system of relatively fast transmission of interoceptive influences to the lumbar motor neurons, which is effective enough to produce a discharge in a large proportion of them. This system is not organized in accordance with the reciprocal principle, and it may cause excitation of both the flexor and the extensor motor neurons of the lower limbs. However, this system is under the tonic inhibitory control of certain brain structures, and its activity is considerably depressed when the nervous system is intact. Several of these inhibitory systems have now been studied in some detail, controlling the spinal reflex arcs (for example, the inhibitory control exerted by certain parts of the reticular formation on synaptic transmission in segmentary polysynaptic arcs [6]).

A special study is required to ascertain which centers exert their inhibitory tonic control on the rapid transmission of visceromotor influences and what afferent influences can modify this control. It may be supposed that this system is identical with or similar to the reticular system which controls the transmission of influences from the splanchnic nerve to the intercostal motor neurons, the exclusion of which leads to marked facilitation of the viscero-intercostal reflexes [4]. However, it is evidently located in the reticular formation not only of the medulla, but also of higher levels of the central nervous system, for its action can be considerably weakened by division of the spinal cord in the cervical region and of the brain at the level of the corpora quadrigemina.

Interruption of the connections between the spinal cord and the brain leads not only to removal of the descending inhibitory influences, but also to the disappearance of a particular group of visceromotor reflexes distinguished in intact animals by a long latent period and duration and by a synaptic organization analogous to that of the flexor reflex. Since these reflexes are well marked in decerebrate animals, there is reason to suppose that they are mediated through the suprasegmentary structures of the rhombencephalon. It is improbable that the disappearance of this group of influences after transection of the spinal cord would be due to other causes (shock, for example), for even with a very large increase in the reflex excitability of the spinal cord after injection of strychnine, no signs of their recovery were observed.

Both mechanisms of interoceptive activation of the motor neurons, spinal and supraspinal, are associated with a simultaneous and marked depolarization of the central endings of the somatic afferent fibers. As a result of the presynaptic inhibition of synaptic transmission, depolarization of this type may evidently weaken the effectiveness of the flow of somatic afferent impulses at a time when an intensive stream of interoceptive influences is arriving in the spinal cord. The onset of presynaptic depolarization, produced by spinal mechanisms, is also inhibited by descending influences from the suprasegmentary structures of the brain. However, this inhibition is not completely identical with the inhibitory control of the synaptic influences on the motor neurons, for it is disturbed by decerebration. The possibility is that the system of internuncial neurons [5] creating presynaptic depolarization is under the control of a special descending apparatus which is different from the apparatus controlling the postsynaptic processes.

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